

New *Aquilariomycetes* and *Mangifericomycetes* species (Pleosporales, Ascomycota) from *Aquilaria* spp. in China

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Abstract

Saprobic fungi are known for their critical role in decomposition and nutrient cycling. The study of saprobic fungi is equally important, as it helps in understanding their ecological roles and identifying their hidden diversity. This study focused on saprobic fungi on *Aquilaria*, which is poorly studied compared to economically important hosts like coffee, tea, and rubber. Our rigorous process led to the collection of two new terrestrial saprobic fungi from the Guangdong and Yunnan provinces in China. After extensive phylogenetic analyses and detailed comparison of morphological characteristics, the two collections were identified as two new species belonging to Pleosporales, Ascomycota. *Aquilariomycetes maomingensis* sp. nov. was isolated from *Aquilaria sinensis* in Guangdong Province, while *Mangifericomys aquilariae* sp. nov. was isolated from *Aquilaria* sp. in Yunnan Province. Full descriptions, photo plates, and phylogenetic analyses (maximum likelihood and Bayesian inference analyses based on LSU, ITS, SSU, tef1-a, and rpb2 gene combinations) of the new species are provided, along with a comprehensive list of saprobic fungi associated with *Aquilaria* spp.

Key words: 2 new species, agarwood, saprobes, Thymelaeaceae, Thyridariaceae

Introduction

Aquilaria Lam. (Thymelaeaceae) is the main plant genus capable of producing agarwood (Lee and Mohamed 2016; Wang et al. 2018; Li et al. 2021). Currently, there are 21 accepted species in *Aquilaria*, of which 13 have been reported to produce agarwood (Hashim et al. 2016). These trees are tropical and subtropical evergreen broad-leaved trees (Rasool and Mohamed 2016; Xu et al. 2016), widely distributed in Asia, such as Borneo, Cambodia, China, India, Indonesia, Laos, Malaysia, New Guinea, the Philippines, Thailand, and Vietnam, (Wang et

al. 2018; 2019). In China, *Aquilaria sinensis* is the primary source of agarwood resin (National Pharmacopoeia Committee 2020).

In recent years, a large number of articles have been published on fungi related to *Aquilaria* and agarwood, and it has been found that fungal induction can effectively induce the production of agarwood (Laurence 2013; Liu et al. 2013; Azren et al. 2018; Chen et al. 2018; Subasinghe et al. 2019; Tibpromma et al. 2021; Du et al. 2022a). Du et al. (2022a,b) reported endophytic fungi from agarwood, with the majority belonging to Ascomycota Caval.-Sm. (mainly from *Botryosphaeria* spp., *Fusarium* spp., and *Lasiodiplodia* spp.). In addition, as an important economic plant, the pathogenic fungi of *Aquilaria* have also been extensively studied, and the reported pathogenic fungi mainly belong to Ascomycota, which cause damage to different parts of trees, such as seedling anthracnose (e.g., *Colletotrichum fructicola* Prihast., L. Cai & K.D. Hyde), dieback (e.g., *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl.), and leaf spot disease (e.g., *Corynespora cassiicola* (Berk. & M.A. Curtis) C.T. Wei) (Borah et al. 2012; Fan et al. 2013; Liao et al. 2018). However, the saprobic fungi of *Aquilaria* have received very little attention. Initially, most saprobic fungi were introduced only based on morphological characteristics, but without molecular data. Du et al. (2022c) initiated exploring and investigating the saprobic fungi of *Aquilaria* spp. based on both morphological and molecular evidence. Some saprobic fungi have recently been discovered on *Aquilaria* spp. in China (Du et al. 2022c, 2023, 2024a, b; Manawasinghe et al. 2024; Tao et al. 2024; Zhang et al. 2024). So far, there are 34 records of saprobic fungi associated with *Aquilaria*, while these saprobes almost all belong to Ascomycota (Du et al. 2024b).

Saprobic fungi, an important component of ecosystems, participate in the carbon cycle by decomposing organic matter (Šnajdr et al. 2011; Li et al. 2022; Niego et al. 2023a). As decomposers, they dominate the litter layer in all forest ecosystems (e.g., tropical, subtropical, temperate, and boreal forests) (Li et al. 2022; Niego et al. 2023b). With increasing attention to ecosystems, extensive research has been conducted on saprobic fungi associated with various plants in recent years. Over 800 taxa have been reported on rubber, of which over half were isolated from leaf and branch litter (Senwanna et al. 2021; Nizamani et al. 2023; Xu et al. 2024). Tian et al. (2024) recently reported 77 saprobic fungi from coconut, pineapple, and rice. In contrast, only 34 records of saprobic fungi are linked to *Aquilaria* spp.; thus, further investigations are required to address this knowledge gap.

In this study, we introduce two new ascomycete species, *Aquilariomycetes mao-mingensis* (Thyridariaceae, Pleosporales) and *Mangifericomes aquilariae* (Pleosporales genus *incertae sedis*, Wijayawardene et al. 2022; Hyde et al. 2024a) based on morphological studies and multilocus phylogenetic analyses. Comprehensive descriptions, photo plates of macro- and micro-morphological characteristics, and phylogenetic analyses highlighting the placement of new taxa are provided. In addition, a list of *Aquilaria*-associated saprobic fungi is provided.

Materials and methods

Sampling, examination, and isolation

Specimens were collected from agarwood (*Aquilaria* spp.) plantations in Guangdong and Yunnan provinces, China, and the necessary information was recorded (Rathnayaka et al. 2024). Each specimen was put in plastic bags, recorded

collection information, and then transported to the laboratory at Qujing Normal University. Morphological characteristics were examined using an OPTEC SZ650 dissecting stereomicroscope (Chongqing, China), and fungal microstructures were observed and photographed using an OLYMPUS DP74 (Tokyo, Japan) digital camera on an OLYMPUS optical microscope (Tokyo, Japan). Morphological structures were measured in the Tarosoft® Image Framework program v. 1.3, and photo plates were edited in Adobe Photoshop CS3 Extended version 22.0.0 software (Adobe Systems, California, the USA).

Single-spore isolation technique was performed according to the description by Senanayake et al. (2020). The fruiting bodies were cut using sterile blades, and sterile needles were used to pick out the ascospores and place them in ddH₂O on a glass slide. The ascospores in the water were dispersed into a spore suspension and transferred to potato dextrose agar (PDA) for culture at 23–28 °C for 12–48 hours. Then, the single germinated ascospores were picked up and transferred to a new PDA with recording culture characters.

Specimens were deposited at the Guizhou Medical University (**GMB-W**) and Mycological Herbarium of Zhongkai University of Agriculture and Engineering (**MHZU**), China. Living cultures were deposited in the Guizhou Medical University Culture Collection (**GMBCC**), Guizhou Culture Collection (**GZCC**), and Zhongkai University of Agriculture and Engineering Culture Collection (**ZHKUCC**), China. Facesoffungi (FoF) numbers were registered as described in Jayasiri et al. (2015), and MycoBank numbers (MB) were registered as outlined in MycoBank (<http://www.MycoBank.org>).

DNA extraction, PCR amplification, and sequencing

Molecular studies were carried out according to Tian et al. (2024). Total genomic DNA was extracted from one-month-old fresh fungal mycelium cultured in PDA using a DNA Extraction Kit-BSC14S1 (BioFlux, Hangzhou, P.R. China), following the manufacturer's instructions. The extracted DNA was stored at 4 °C for the polymerase chain reaction (PCR), while the remaining DNA was maintained at -20 °C for long-term storage. The PCR mixture (25 µL) contains 12.5 µL of 2xMaster Mix (mixture of Easy Taq TM DNA Polymerase, dNTPs, and optimized buffer (Beijing Trans Gen Biotech Co., Chaoyang District, Beijing, China)), 8.5 µL of ddH₂O, and 1 µL of each forward and reverse primer (10 pM) and 2 µL of DNA template (Tibpromma et al. 2018). The PCR was carried out using the following primers: The internal transcribed spacer (ITS) region was amplified with the primers ITS4 and ITS5 (White et al. 1990); the 28S large subunit (LSU) region was amplified using the primers LR0R and LR5 (Vilgalys and Hester 1990); the 18S small subunit (SSU) region was amplified using the primers NS1 and NS4 (White et al. 1990); the partial translation elongation factor1-alpha (*tef1-a*) gene was amplified using the primers EF1-983F and EF1-2218R (Rehner 2001); and the partial RNA polymerase II subunit (*rpb2*) region was amplified with primers fRPB2-5F and fRPB2-7cR (Liu et al. 1999). The PCR thermal cycle programs for LSU, ITS, SSU, and *tef1-a* were as follows: an initialization step of 94 °C for 3 min, followed by 35 cycles of 94 °C for 30 s, an annealing step at 55 °C for 50 s, an elongation step at 72 °C for 1 min, and a final extension step of 72 °C for 10 min; and the PCR thermal cycle programs for *rpb2* were as follows: an initialization step of 95 °C for 3 min, followed by 40 cycles of 95 °C for 50 s, an annealing

step at 57 °C for 50 s, an elongation step at 72 °C for 90 s, and a final extension step of 72 °C for 10 min. Purification and sequencing of PCR products were carried out using the same primers by Sangon Biotech Co., Kunming, China.

Phylogenetic analyses

Phylogenetic analyses were carried out according to Dissanayake et al. (2020). Both reverse and forward sequences generated in this study were assembled using Geneious 9.1.8 (<https://www.geneious.com>) (Kearse et al. 2012), and newly generated sequences were searched using the BLASTn in NCBI (https://blast.ncbi.nlm.nih.gov/Blast.cgi?PAGE_TYPE=BlastSearch) to identify the most similar taxa. The additional sequences included in the analyses were collected from recent publications (Yang et al. 2022; Du et al. 2024b) and downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/WebSub/?form=history&tool=genbank>). The FASTA file was created using the OFPT (Zeng et al. 2023) with the protocol used for constructing the Randomized Accelerated Maximum Likelihood (RAxML) and Bayesian Inference analyses (BI). Then FASTA format was converted to PHYLIP (for RAxML) and NEXUS formats (for BI), respectively, using ALTER (<http://www.sing-group.org/ALTER/>) (Glez-Peña et al. 2010).

The RAxML was generated on the CIPRES Science Gateway (<https://www.phylo.org/portal2/login!input.action>) (Miller et al. 2010), using RAxML-HPC2 on XSEDE (8.2.12) with 1,000 bootstrap replicates (Stamatakis et al. 2008; Stamatakis 2014) and the GTR+I+G model of evolution and bootstrap supports. The BI tree was performed with MrBayes on XSEDE (3.2.7a) (Ronquist et al. 2012), and the best models of evolution were estimated using MrModeltest v. 2.3 (Nylander et al. 2008). Six simultaneous Markov chains were run for 1,000,000 to 2,000,000 generations, and the tree was sampled every 100th generation. The phylogenetic tree was visualized in FigTree v.1.4.2 (Rambaut 2012) and edited by Microsoft Office PowerPoint 2021 and Adobe Photoshop CS3 Extended version 22.0.0 software (Adobe Systems, California, the USA). All newly generated sequences in this study were deposited to GenBank (<https://www.ncbi.nlm.nih.gov/WebSub/?form=history&tool=genbank>).

A list of saprobic fungi associated with *Aquilaria*

A list of reported saprobic fungi associated with *Aquilaria* spp. is listed in Table 1, and the percentage of different classes is shown in Fig. 1, which includes two new species introduced in this study. This list includes the host and distributions, molecular data, and relevant references of *Aquilaria*-associated saprobic fungi.

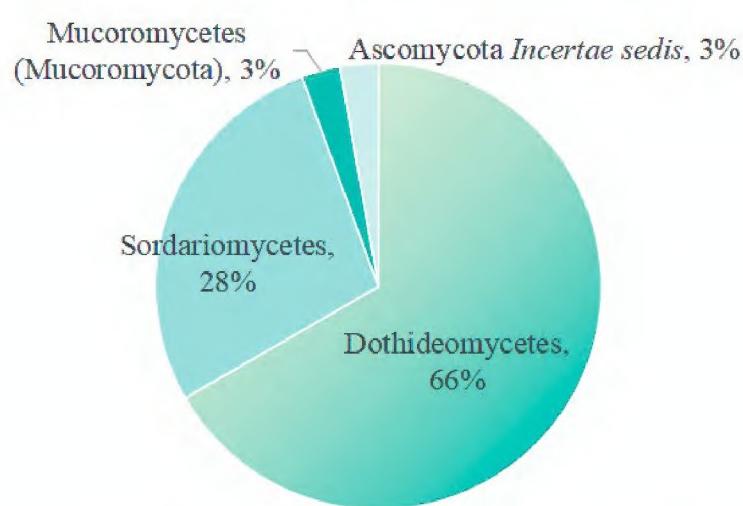


Figure 1. *Aquilaria* spp.-associated saprobic fungi in different classes and *incertae sedis*.

Table 1. A list of saprobic fungi reported on *Aquilaria* spp.

Host species	Host countries	Phylum	Class	Fungal species	Molecular data	References
<i>A. agallocha</i>	Bangladesh	Ascomycota	Sordariomycetes	<i>Phomopsis aquilariae</i>	NA	Punithalingam and Gibson 1978
<i>A. sinensis</i>	China	Ascomycota	Sordariomycetes	<i>Allocryptovalsa aquilariae</i>	ITS and TUB	Chethana et al. 2023
<i>A. sinensis</i>	China	Ascomycota	Dothideomycetes	<i>Aquilariomycetes maomingensis</i>	ITS, LSU, SSU, tef1-a, and rpb2	This study
<i>A. sinensis</i>	China	Ascomycota	Dothideomycetes	<i>Barriopsis stevensiana</i>	ITS, LSU, SSU, and tef1-a	Hyde et al. 2024c
<i>A. sinensis</i>	China	Ascomycota	Dothideomycetes	<i>Camarographium clematidis</i>	ITS, LSU, SSU, and tef1-a	Du et al. 2024b
<i>A. sinensis</i>	China	Ascomycota	Dothideomycetes	<i>Melomastia aquilariae</i>	LSU, SSU, and tef1-a	Manawasinghe et al. 2024
<i>A. sinensis</i>	China	Ascomycota	Dothideomycetes	<i>Melomastia guangdongensis</i>	LSU, SSU, and tef1-a	Du et al. 2024a
<i>A. sinensis</i>	China	Ascomycota	Dothideomycetes	<i>Melomastia maomingensis</i>	ITS, LSU, SSU, tef1-a, and rpb2	Du et al. 2024b
<i>A. sinensis</i>	China	Ascomycota	Dothideomycetes	<i>Montagnula aquilariae</i>	ITS, LSU, SSU, and tef1-a	Hyde et al. 2023
<i>A. sinensis</i>	China	Ascomycota	Dothideomycetes	<i>Nigrograna aquilariae</i>	ITS, LSU, SSU, tef1-a, and rpb2	Du et al. 2024b
<i>A. sinensis</i>	China	Ascomycota	Sordariomycetes	<i>Peroneutypa aquilariae</i>	ITS and TUB	Du et al. 2022c
<i>A. sinensis</i>	China	Ascomycota	Sordariomycetes	<i>Peroneutypa maomingensis</i>	ITS, LSU, SSU, tef1-a, rpb2, and TUB	Du et al. 2024b
<i>A. sinensis</i>	China	Ascomycota	Dothideomycetes	<i>Pseudothyridariella aquilariae</i>	ITS, LSU, SSU, tef1-a, and rpb2	Du et al. 2024b
<i>A. sinensis</i>	China	Ascomycota	Dothideomycetes	<i>Rhytidhysteron thailandicum</i>	ITS, LSU, SSU, and tef1-a	Du et al. 2023
<i>A. sinensis</i>	China	Ascomycota	Sordariomycetes	<i>Triangularia aquilariae</i>	ITS, LSU, SSU, rpb2, and TUB	Du et al. 2024b
<i>A. sinensis</i>	China	Ascomycota	Sordariomycetes	<i>Allocryptovalsa rabenhorstii</i>	ITS and TUB	Hyde et al. 2024c
<i>Aquilaria</i> sp.	China	Ascomycota	Sordariomycetes	<i>Allocryptovalsa castaneae</i>	ITS and TUB	Zhang et al. 2024
<i>Aquilaria</i> sp.	Thailand	Ascomycota	Dothideomycetes	<i>Cercospora</i> sp.	NA	Subansenee et al. 1985
<i>Aquilaria</i> sp.	Thailand	Ascomycota	Sordariomycetes	<i>Chaetomium spirale</i>	NA	Subansenee et al. 1985
<i>Aquilaria</i> sp.	Thailand	Ascomycota	Dothideomycetes	<i>Cladosporium</i> sp.	NA	Subansenee et al. 1985
<i>Aquilaria</i> sp.	China	Ascomycota	Dothideomycetes	<i>Mangifericomes aquilariae</i>	ITS, LSU, SSU, tef1-a, and rpb2	This study
<i>Aquilaria</i> sp.	China	Ascomycota	Dothideomycetes	<i>Melomastia clematidis</i>	LSU, SSU, and tef1-a	Tao et al. 2024
<i>Aquilaria</i> sp.	China	Ascomycota	Dothideomycetes	<i>Melomastia sinensis</i>	LSU, SSU, and tef1-a	Du et al. 2024a
<i>Aquilaria</i> sp.	China	Ascomycota	Dothideomycetes	<i>Melomastia winteri</i>	LSU, SSU, and tef1-a	Hyde et al. 2024c
<i>Aquilaria</i> sp.	China	Ascomycota	Dothideomycetes	<i>Melomastia yunnanensis</i>	LSU, SSU, and tef1-a	Du et al. 2024a
<i>Aquilaria</i> sp.	China	Ascomycota	Dothideomycetes	<i>Nigrograna magnoliae</i>	ITS, LSU, SSU, and tef1-a	Hyde et al. 2024c
<i>Aquilaria</i> sp.	Thailand	Ascomycota	Sordariomycetes	<i>Phialogeniculata</i> sp.	NA	Subansenee et al. 1985
<i>Aquilaria</i> sp.	Thailand	Ascomycota	Dothideomycetes	<i>Pithomyces</i> sp.	NA	Subansenee et al. 1985
<i>Aquilaria</i> sp.	China	Ascomycota	<i>Incertae sedis</i>	<i>Pseudoacrodictys deightonii</i>	ITS, LSU, SSU, and TUB	Hyde et al. 2024c
<i>Aquilaria</i> sp.	Thailand	Mucoromycota	Mucoromycetes	<i>Rhizopus</i> sp.	NA	Subansenee et al. 1985
<i>Aquilaria</i> sp.	China	Ascomycota	Dothideomycetes	<i>Thyridaria aureobrunnea</i>	ITS, LSU, tef1-a, and rpb2	Hyde et al. 2024c
<i>Aquilaria</i> sp.	Thailand	Ascomycota	Sordariomycetes	<i>Trichoderma</i> sp.	NA	Subansenee et al. 1985
<i>A. yunnanensis</i>	China	Ascomycota	Dothideomycetes	<i>Aquilariomycetes aquilariae</i>	ITS, LSU, SSU, tef1-a, and rpb2	Du et al. 2024b
<i>A. yunnanensis</i>	China	Ascomycota	Dothideomycetes	<i>Corynespora aquilariae</i>	ITS, LSU, SSU, and tef1-a	Du et al. 2024b
<i>A. yunnanensis</i>	China	Ascomycota	Dothideomycetes	<i>Parathyridariella aquilariae</i>	ITS, LSU, SSU, and rpb2	Du et al. 2024b
<i>A. yunnanensis</i>	China	Ascomycota	Dothideomycetes	<i>Phaeoseptum aquilariae</i>	ITS, LSU, SSU, tef1-a, and rpb2	Du et al. 2024b

Notes: NA = Sequence unavailability.

Results

Taxonomy

Thyridariaceae Q. Tian & K.D. Hyde, 2013

Aquilariomycetes T.Y. Du, Tibpromma & Karun. 2024

Notes. *Aquilariomycetes* was introduced by Du et al. (2024b) as a monotypic genus to accommodate *Aq. aquilariae* T.Y. Du, Tibpromma & Karun. as the

type species, which was collected from *Aquilaria yunnanensis* S.C. Huang in Yunnan Province, China. Based on well-separated phylogenetic branches and unique sexual morphs of ascospores, *Aquilariomycetes* was introduced as a new genus in Thyridariaceae (Du et al. 2024b). This genus is characterized by globose to subglobose, brown to dark brown, solitary or gregarious ascomata in small groups, immersed under the bark, surrounded by brown to black fluffs; a peridium comprising hyaline to brown cells of ***texturaria angularis***; hyaline septate, branched, trabeculate pseudoparaphyses, embedded in a gelatinous matrix; 8-spored, bitunicate, clavate, apically rounded ascospores, surrounded by mucilaginous sheath, while the asexual morph is not reported. The updated phylogenetic tree of *Aquilariomycetes* is shown in Fig. 2.

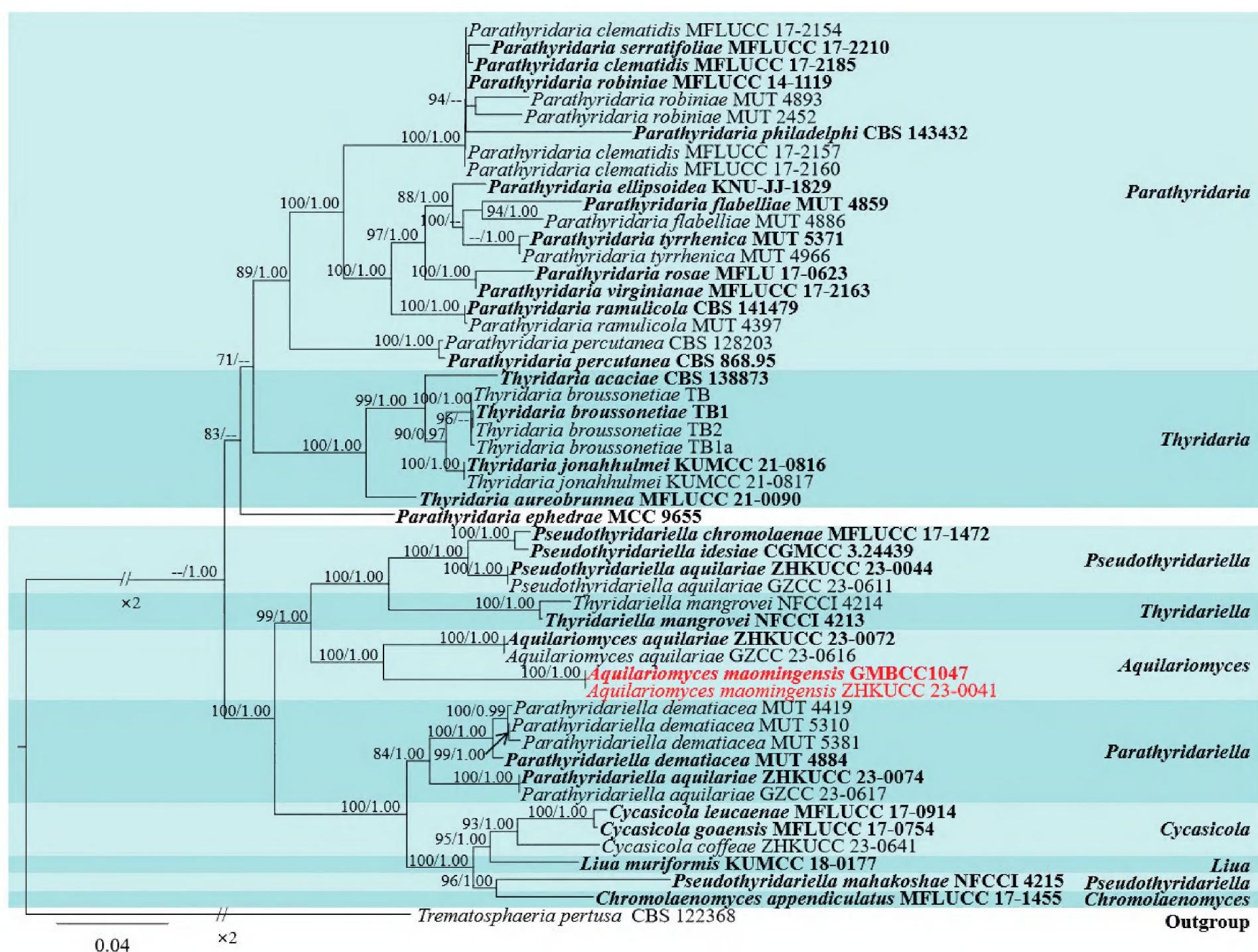


Figure 2. Phylogram generated from maximum likelihood (ML) analysis based on combined LSU, ITS, SSU, tef1-a, and *rpb2* sequence data of 52 taxa, which comprised 4387 base pairs of LSU = 967, ITS = 516, SSU = 872, *rpb2* = 1024, tef1-a = 1008. The best-scoring RAxML tree with a final likelihood value of -31596.745436 is presented. The matrix had 2090 distinct alignment patterns, with 47.13% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.249245, C = 0.257277, G = 0.271627, T = 0.221851; substitution rates: AC = 1.210949, AG = 2.948777, AT = 1.318881, CG = 0.897105, CT = 6.444599, GT = 1.0; gamma distribution shape parameter α = 0.441696. Bootstrap support values for ML equal to or greater than 70% and clade credibility values equal to or greater than 0.90 from Bayesian inference analysis are labelled at each node. The tree is rooted with *Trematosphaeria pertusa* (CBS 122368). The new isolates are indicated in red, and the ex-type strains are in bold.

***Aquilariomyces maomingensis* T.Y. Du, K.D. Hyde, Tibpromma & Karun., sp. nov.**

Mycobank No: 856409

Facesoffungi Number: FoF16960

Fig. 3

Etymology. Named after the location “Maoming,” where the holotype was collected.

Holotype. MHZU 23-0022.

Description. **Saprobic** on decaying branch of *Aquilaria sinensis*. **Sexual morph:** **Ascomata** (excluding necks) 250–450 µm high × 200–500 µm diam. ($\bar{x} = 366 \times 350$ µm, n = 5), solitary or gregarious in small groups, brown to dark brown, surrounded by short brown to black fluffs, immersed, slightly raised under the bark, globose to subglobose, sometimes ovoid, ostiolate. **Ostiolar canal** 250–280 µm long × 150–200 µm wide ($\bar{x} = 263 \times 180$ µm, n = 10), cylindrical to elliptical, usually straight, dark brown to black necks with periphyses. **Peridiolum** 15–70 µm ($\bar{x} = 31$ µm, n = 30) wide, comprising 3–5 layers of pale brown to brown cells of **textura angularis** to **textura prismatica**, fusing with the host tissue. **Hamathecium** comprising 1 µm wide, hyaline, septate, branched, numerous, trabeculate pseudoparaphyses (*sensu* Liew et al. 2000), embedded in a gelatinous matrix. **Asci** 100–140 × 21–25 µm ($\bar{x} = 123 \times 23$ µm, n = 30), bitunicate, 8-spored, thick-walled, clavate, apically rounded, with an ocular chamber, short pedicel, some club-shaped. **Ascospores** 20–36 × 9–15 µm ($\bar{x} = 30 \times 13$ µm, n = 30), uniseriate, 1-septate, fusiform to ellipsoidal, conical at both ends or round, constricted at the septum, upper cells are slightly larger than below cells, rough-walled, with several guttules and granules, hyaline to pale yellow when immature and surrounded by a mucilaginous sheath, later become yellow-brown and without a mucilaginous sheath. **Asexual morph:** Undetermined.

Culture characteristics. Ascospores germinated on PDA after 12 hours, and germ tubes were produced from one or both ends. **Colonies** on PDA reaching 2–3 cm diam. after two weeks at 23–28 °C. Colonies obverse: dense, circular, or irregular, cream to brown, umbonate, raised at the center, filamentous edge. Colonies reverse dark brown to black at the center and cream to light brown at the margin.

Material examined. CHINA • Guangdong Province, Maoming City, Dianbai District, Poxin Town, 21°34'25"N, 111°7'43"E, on a dead branch of *Aquilaria sinensis* (Thymelaeaceae), 3 June 2022, T.Y. Du, MMA15 (MHZU 23-0022, holotype), ex-type living culture, GMBCC1047; additional living culture, ZHKUCC 23-0041.

GenBank numbers. GMBCC1047: ITS = PQ604643, LSU = PQ604620, SSU = PQ604624, tef1-a = PQ612415, rpb2 = PQ612419; ZHKUCC 23-0041: ITS = PQ604644, LSU = PQ604621, SSU = PQ604625, tef1-a = PQ612416, rpb2 = PQ612420.

Notes. In the present phylogenetic analyses, our new collection, *Aquilariomyces maomingensis*, formed a well-separated sister lineage to *Aq. aquilariae* (ZHKUCC 23-0072 and GZCC 23-0616) with 100% ML and 1.00 BYPP statistical support (Fig. 2). *Aquilariomyces maomingensis* shares similar morphological characteristics with *Aq. aquilariae* (MHZU 23-0036, holotype) in having immersed, globose to subglobose ascomata, numerous, septate, branched, trabeculate pseudoparaphyses in a gelatinous matrix, clavate ascii, with short and club-shaped pedicel, and uniseriate fusiform to ellipsoidal, 1-septate, ascospores, constricted at the septum, and surrounded by a mucilaginous sheath (Du et al. 2024b). However, *Aq. maomingensis* (MHZU 23-0022) differs from *Aq. aquilariae*

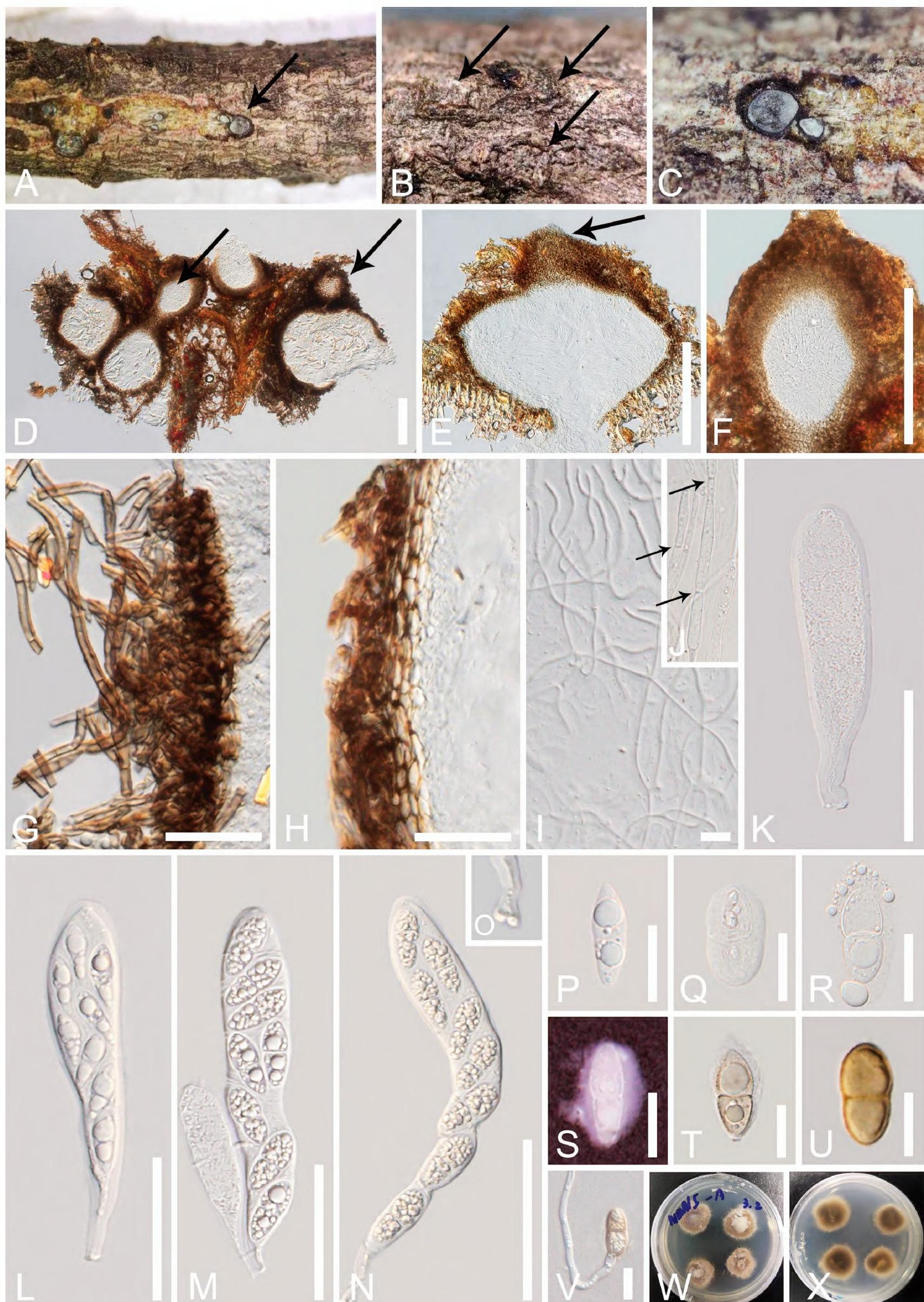


Figure 3. *Aquilariomyces maomingensis* (MHZU 23-0022, holotype) **A–C** appearance of ascomata on the host (the arrows indicate ascomata) **D, E** vertical sections through the ascomata (the arrows indicate ostioles) **F** ostiole with periphyses **G** short fluffs around the periphery of the ascomata **H** peridium **I, J** trabeculae pseudoparaphyses (**J** the arrows indicate septate pseudoparaphyses) **K–N** asci **O** a club-shaped pedicel **P–U** ascospores (**S** stained with Indian ink) **V** germinated ascospore **W, X** colonies on PDA obverse and reverse views. Scale bars: 200 µm (**D–F**); 30 µm (**G, H**); 10 µm (**I**); 50 µm (**K–N**); 20 µm (**P–V**).

(MHZU 23-0036) in its ascocarps and ascospore characters. *Aquilariomycetes maomingensis* has ascocarps surrounded by short fluffs, slightly raised under the bark, and brown mature ascospores, while *Aq. aquilariae* (MHZU 23-0036) has inconspicuous ascocarps, surrounded by long fluffs, and hyaline mature ascospores (Du et al. 2024b). A comparison of the main morphological structures between *Aquilariomycetes maomingensis* and *Aq. Aquilariae* is shown in Fig. 4.

According to the phylogenetic analysis of the present study, both *Aquilariomycetes* species clustered in Thyridariaceae, a family characterized by trabeculate or cellular pseudoparaphyses. Trabeculate pseudoparaphyses are characterized by narrow, thread-like, apparently nonseptate, branched, and anastomosing or unbranched above the asci and embedded in a gelatinous matrix (Liew et al. 2000; Hongsanan et al. 2020). This type of pseudoparaphyses is found in *Aquilariomycetes* (Fig. 3I). Trabeculae were considered important at the Dothideomycetes O.E. Erikss. & Winka in earlier classifications; thus, Melanommatales was defined as having trabeculae (Barr 1983). However, Liew et al. (2000) showed that trabeculae were not important at the order level and probably were important at the family level (or even species). Thyridariaceae comprises nine genera: *Aquilariomycetes*, *Chromolaenomyces* Mapook & K.D. Hyde, *Cycasicola* Wanas., E.B.G. Jones & K.D. Hyde, *Liua* Phookamsak & K.D. Hyde, *Parathyridaria* Jaklitsch & Voglmayr, *Parathyridariella* Prigione, A. Poli, E.

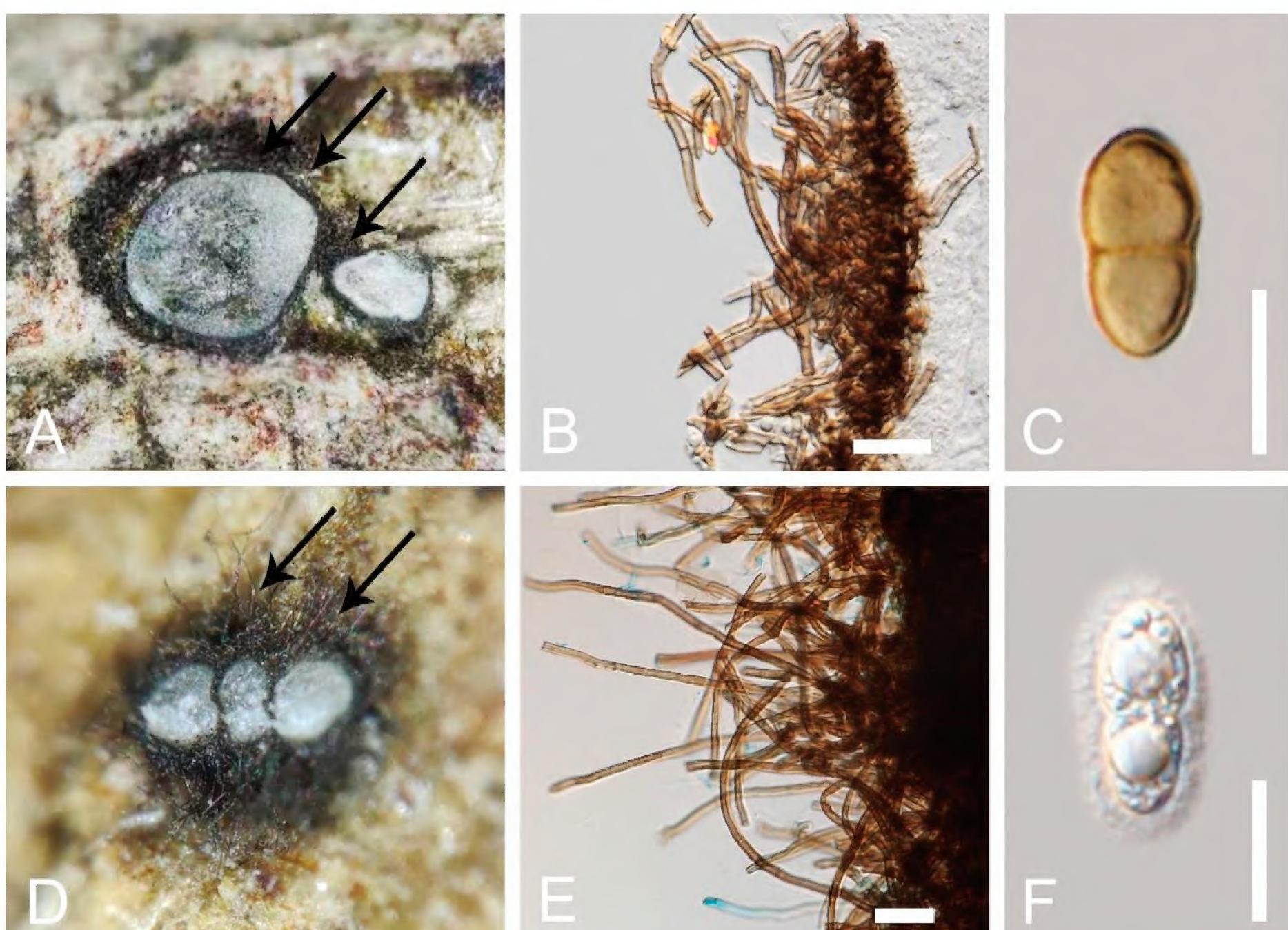


Figure 4. Comparison of morphological structure between *Aquilariomycetes maomingensis* and *Aq. aquilariae*. *Aquilariomycetes maomingensis* (MHZU 23-0022 holotype) **A** ascocarps wrapped in short fluffs **B** micrograph of fluffs **C** brown ascospores. *Aquilariomycetes aquilariae* (MHZU 23-0036, holotype) (Du et al. 2024b) **D** ascocarps wrapped in long fluffs **E** micrograph of fluffs **F** hyaline ascospores. Scale bars: 20 µm (**B, C, E, F**).

Bovio & Varese, *Pseudothyridariella* Mapook & K.D. Hyde, *Thyridaria* Sacc., and *Thyridariella* Devadatha, V.V. Sarma, K.D. Hyde, Wanas. & E.B.G. Jones (Wijayawardene et al. 2022; Du et al. 2024b). Among these genera, *Aquilariomyces* (Du et al. 2024b), *Parathyridaria* (Jaklitsch and Voglmayr 2016), and *Thyridaria* (Jaklitsch and Voglmayr 2016) have trabeculate pseudoparaphyses; *Chromolaenomyces* (Mapook et al. 2020), *Pseudothyridariella* (Mapook et al. 2020), and *Thyridariella* (Devadatha et al. 2018) have cellular pseudoparaphyses, while pseudoparaphyses of this type have not been reported yet in other genera, viz. *Cycasicola*, *Liua*, and *Parathyridariella*. We believe pseudoparaphyses type is one of the important characters at the genus level.

The base pair differences in the LSU, ITS, SSU, *tef1-a*, and *rpb2* genes (without gaps) between our new collection and *Aq. aquilariae* (ZHKUCC 23-0072, ex-type) were also compared. The results showed that there are 3.1% nucleotide differences (28/912 bp) in LSU; in comparison, ITS has 12.3% nucleotide differences (67/544 bp), SSU has 0.3% nucleotide differences (3/873 bp), *tef1-a* has 7.5% nucleotide differences (76/1008 bp), and *rpb2* has 10.6% nucleotide differences (109/1025 bp). These comparisons indicate minor differences in SSU and LSU, while there are considerable base differences in ITS, *tef1-a*, and *rpb2*. Therefore, we introduce our new collection as a new species, *Aq. maomingensis*, based on a polyphasic approach, according to the guidelines of Maharachchikumbura et al. (2021). *Aquilariomyces maomingensis*, the second *Aquilariomyces* species, was collected from the same host genus and country (*Aquilaria sinensis*, China) as the first.

Pleosporales genera *incertae sedis*

***Mangifericomes* E.F. Yang & Tibpromma, 2022**

Notes. *Mangifericomes* was established by Yang et al. (2022) as a monotypic genus in the Pleosporales genera *incertae sedis* to accommodate *M. hongheensis* E.F. Yang and Tibpromma as type species, which was isolated from *Mangifera indica* L. in China. *Mangifericomes* is characterized by immersed or semi-immersed, globose to subglobose, dark brown to black ascomata with or without ostioles; a hamathecium comprising filiform, hyaline, septate, branched cellular pseudoparaphyses (*sensu* Liew et al. 2000); 8-spored, bitunicate, cylindrical-clavate, pedicellate asci; and ellipsoid, muriform, pale brown to brown ascospores, wrapped in a gelatinous sheath (Yang et al. 2022). The updated phylogenetic tree of *Mangifericomes* is shown in Fig. 5.

***Mangifericomes aquilariae* T.Y. Du, K.D. Hyde, Tibpromma & Karun., sp. nov.**

MycoBank No: 856410

Facesoffungi Number: FoF16961

Fig. 6

Etymology. Named after the host genus “*Aquilaria*,” from which the holotype was collected.

Holotype. GMB-W 1008.

Description. **Saprobic** on decaying branch of *Aquilaria* sp. **Sexual morph:** **Ascomata** 280–460 µm high × 250–510 µm diam. ($\bar{x} = 375 \times 380$ µm, n = 10),

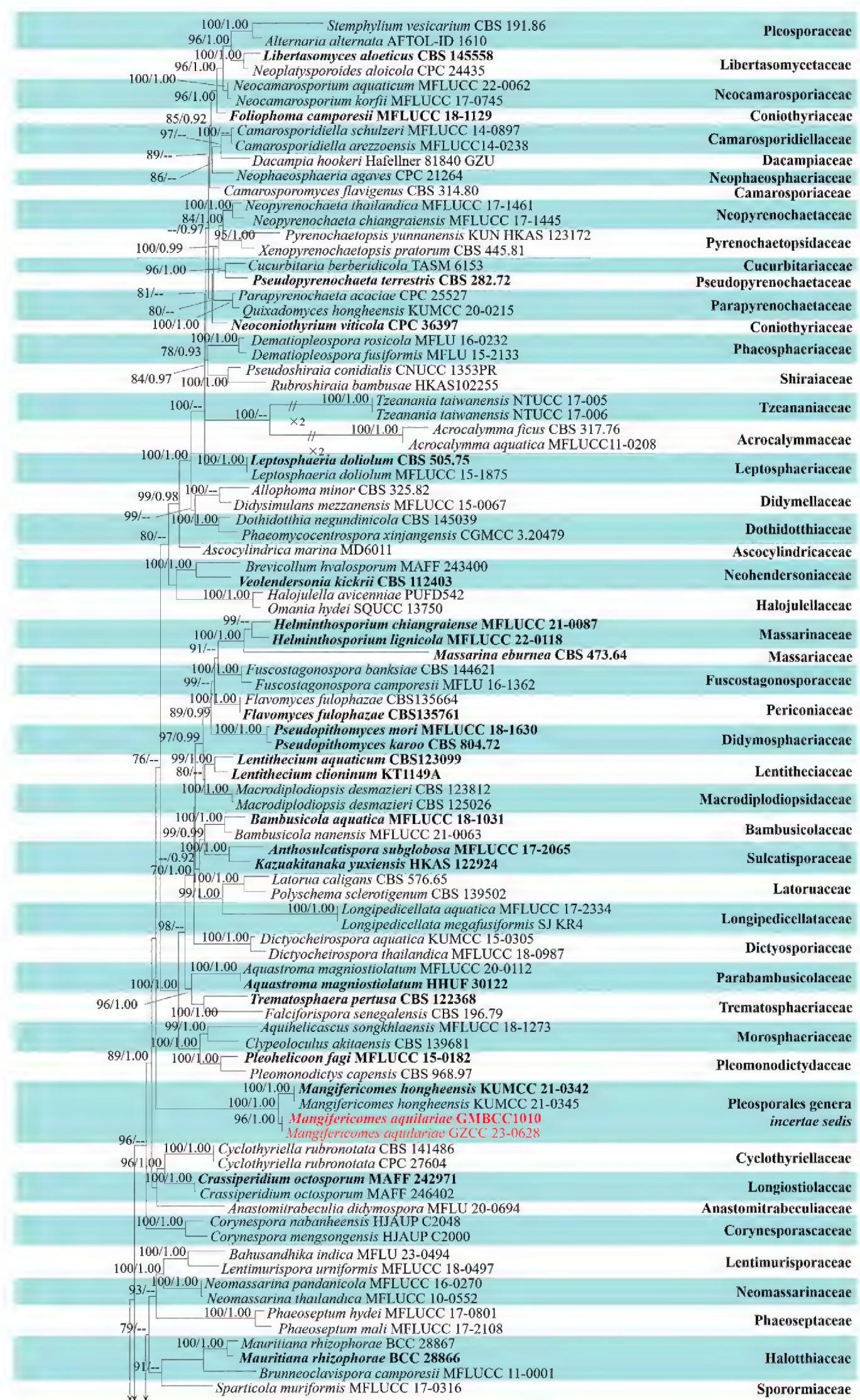


Figure 5. Phylogram generated from ML analysis of Pleosporales based on combined LSU, ITS, SSU, tef1-a, and *rpb2* sequence data of 159 taxa, which comprised 4584 base pairs of LSU = 1201, ITS = 534, SSU = 1018, *rpb2* = 930, tef1-a = 901. The best-scoring RAxML tree with a final likelihood value of -91408.743991 is presented. The matrix had 3121 distinct alignment patterns, with 41.32% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.246701, C = 0.244302, G = 0.274425, T = 0.234571; substitution rates: AC = 1.391138, AG = 3.919388, AT = 1.582417, CG = 1.094328, CT = 7.887132, GT = 1.0; gamma distribution shape parameter α = 0.418663. Bootstrap support values for maximum likelihood (ML) equal to or greater than 70% and clade credibility values equal to or greater than 0.90 from Bayesian inference analysis are labelled at each node. The tree is rooted with *Orbilia auricolor* (AFTOL-ID 906) and *O. vinosa* (AFTOL-ID 905). The new isolates are indicated in red, and the ex-type strains are in bold.

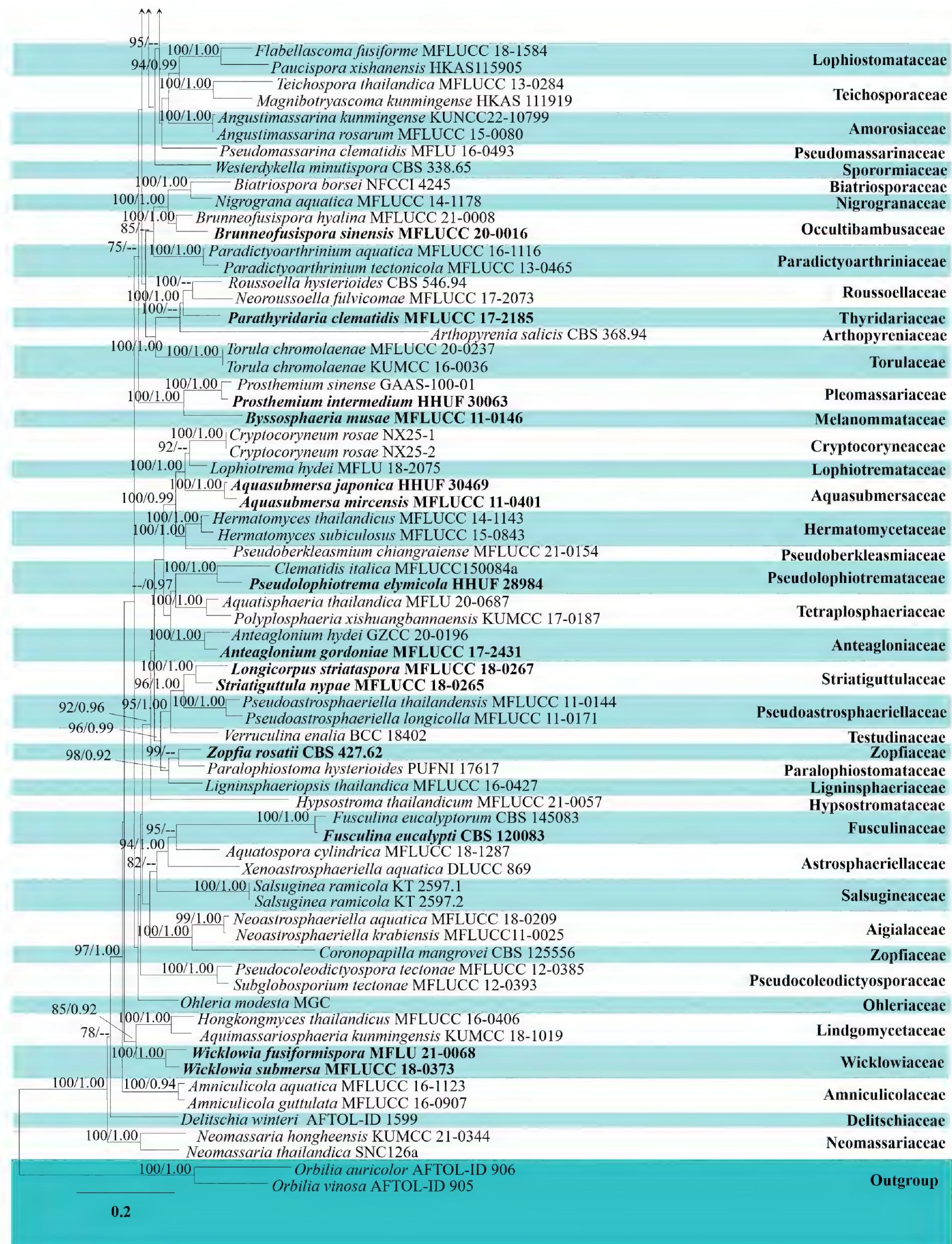


Figure 5. Continued

globose to subglobose, brown to dark brown, gregarious, immersed, inconspicuous on host surface, ostiolate. **Peridium** 20–70 µm ($\bar{x} = 40$ µm, $n = 20$) wide, comprising 5–7 layers of hyaline to pale brown cells of **textura angularis** to **tex-**

tura prismatica, fusing with the host tissue. **Hamathecium** 2.5 µm wide, hyaline, fascicular, septate, branched, numerous, cellular pseudoparaphyses, embedded in a glutinous matrix. **Asci** 170–265 × 32–50 µm ($\bar{x} = 216 \times 40$ µm, n = 30), bitunicate, fissitunicate, 8-spored, cylindric-clavate, with short pedicel, apically rounded, with an ocular chamber. **Ascospores** 40–53 × 18–23 µm ($\bar{x} = 47 \times 20$ µm, n = 30), muriform, uniseriate, hyaline and later become golden yellow, pale brown to dark brown, ellipsoid, slightly curved to straight, rough-walled, slightly wider near apex, apically rounded, 10–13-transversally septate, and 3–6-longitudinal septa, slightly constricted at the septum, surrounded by a 6.5–15 µm wide gelatinous sheath. **Asexual morph:** Undetermined.

Culture characteristics. Ascospores germinated on PDA after 24 hours, and germ tubes were produced from each cell. **Colonies** on PDA reaching 5 cm diam., after four weeks at 23–28 °C. Colonies obverse: loose, circular or irregular, white-cream, slightly raised at the center, filamentous edge. Colonies reverse reddish-brown at the center and cream to light yellow towards the periphery.

Material examined. CHINA • Yunnan Province, Nujiang Prefecture, Lushui City, Liuku Town, 25°48'30"N, 98°51'5"E, on a dead branch of *Aquilaria* sp. (Thymelaeaceae), 21 April 2023, T.Y. Du, NJT41 (GMB-W 1008, holotype), ex-type living culture, GMBCC1010; additional living culture, GZCC 23-0628.

GenBank numbers. GMBCC1010: ITS = PQ604645, LSU = PQ604622, tef1-a = PQ612417, rpb2 = PQ612421; GZCC 23-0628: ITS = PQ604646, LSU = PQ604623, tef1-a = PQ612418, rpb2 = PQ612422.

Notes. In the present phylogenetic analyses, our new collection, *Mangifericomae aquilariae*, formed a well-separated sister lineage to *M. hongheensis* (KUMCC 21-0342 and KUMUCC 21-0345) with 100% ML and 1.00 BYPP statistical support (Fig. 5). *Mangifericomae aquilariae* shares similar morphological characteristics with *M. hongheensis* (HKAS 1221888, holotype) in having globose to subglobose, brown to dark brown, ostiolate ascomata, bitunicate ascii with fissitunicate, 8-spored, cylindrical-clavate, and muriform ascospores, ellipsoid, pale brown to dark brown, slightly wider near the apex, surrounded by a gelatinous sheath (Yang et al. 2022). However, *M. aquilariae* (GMB-W 1008) differs from *M. hongheensis* (HKAS 1221888) by its immersed ascomata, peridium comprising ***textura prismatica*** to ***textura angularis*** cells, fascicular, and numerous pseudoparaphyses, and ascospores that are 10–13-transversally septate, 3–6-longitudinal septa, while ascomata of *M. hongheensis* (HKAS 1221888) are semi-immersed to fully immersed, peridium comprising ***textura angularis*** to ***textura globosa*** cells, sparse pseudoparaphyses, and ascospores that are 7–11-transversally septate, 5–8-longitudinal septa (Yang et al. 2022). In addition, the base pair differences of the LSU, ITS, tef1-a, and rpb2 genes (without gaps) between our new collection and *M. hongheensis* (KUMCC 21-0342, ex-type) were compared, while the SSU of our new collection is not available. The results showed that there are 0.8% nucleotide differences (7/864 bp) in LSU, while ITS has 3.4% nucleotide differences (18/533 bp), tef1-a has 3.2% nucleotide differences (31/962 bp), and rpb2 has 4.5% nucleotide differences (41/905 bp). These comparisons indicate that they display minor differences on LSU while displaying significant base differences on ITS, tef1-a, and rpb2. Therefore, we introduce our new collection (from *Aquilaria* sp. in China) as a new species, *M. aquilariae*, based on a polyphasic approach according to the guidelines of Maharrachchikumbura et al. (2021). In addition, this study introduces the second *Mangifericomae* species in the genus and the first *Mangifericomae* species collected from *Aquilaria*.

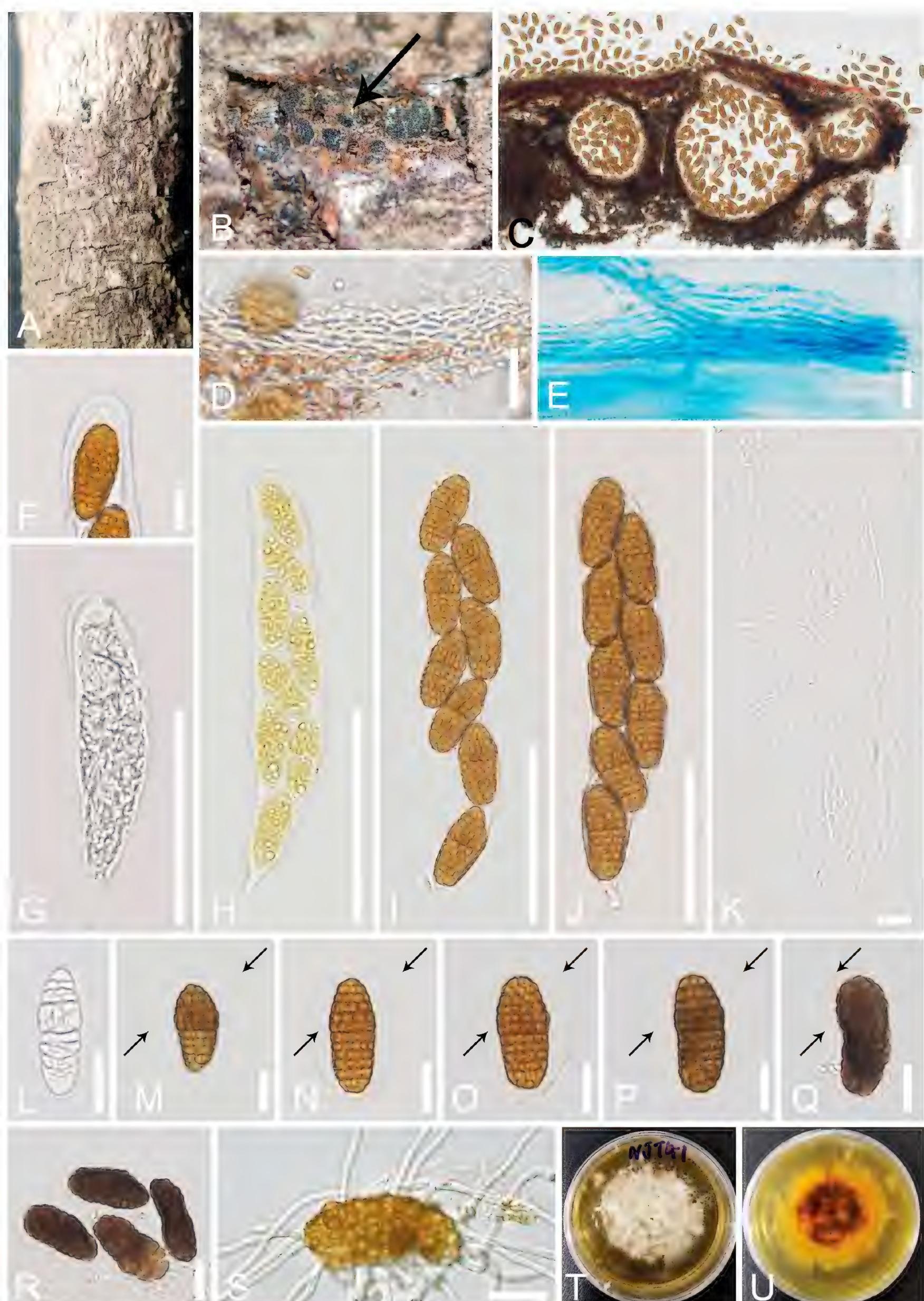


Figure 6. *Mangifercomes aquilariae* (GMB-W 1008, holotype) **A, B** ascomata on the host (the arrow indicates the cross-section of the ascomata) **C** vertical sections through the ascomata **D** peridium **E** cellular pseudoparaphyses (**E** stained with cotton blue) **F** ocular chamber of asci **G–J** asci **L–R** ascospores (the arrows indicate the sheath of the ascospores) **S** germinated ascospore **T, U** colony on PDA obverse and reverse views. Scale bars: 200 µm (**C**); 20 µm (**D, G, L–S**); 10 µm (**E, K**); 100 µm (**F, H–J**).

Discussion

Aquilaria, the primary genus that produces agarwood, is a plant of significant medicinal and economic value, with 13 species known to produce agarwood (Hashim et al. 2016). As Table 1 and Fig. 1 show, saprobic fungi associated with *Aquilaria* mainly belong to Dothideomycetes and Sordariomycetes O.E. Erikss. & Winka of Ascomycota, with only one taxon reported in Mucoromycetes Doweld of Mucoromycota Doweld. This is also consistent in both endophytic and pathogenic fungi of *Aquilaria* spp. (Du et al. 2022a,b). The currently recorded distribution range of these saprobic fungi is mainly in China (28 records, including this study), Thailand (seven records), and only one record in Bangladesh. This is mainly because *Aquilaria* is a tropical tree genus, mainly distributed in tropical regions. Among these records, eight species (*Cercosporaella* sp., *Chaetomium spirale*, *Cladosporium* sp., *Phialogeniculata* sp., *Phomopsis aquilariae*, *Pithomyces* sp., *Rhizopus* sp., and *Trichoderma* sp.) lack molecular data and detailed morphological descriptions. It is necessary to explore saprobic fungi associated with *Aquilaria* spp. with more collections in broader geographical regions.

A thorough investigation and systematic sampling in this study resulted in the authentication of two new species of saprobic fungi on *Aquilaria* from China: *Aquilariomycetes maomingensis* on *Aquilaria sinensis* from Maoming City, Guangdong Province in June 2022, and *Mangifericomes aquilariae* on *Aquilaria* sp. from Nujiang, Yunnan Province in April 2023. In the genus *Aquilariomycetes*, *Aq. aquilariae* was collected from *Aquilaria yunnanensis* in Yunnan Province (Du et al. 2024b). In this study, *Aq. maomingensis* is introduced as the second species in *Aquilariomycetes*, which was collected from *Aquilaria sinensis* in Guangdong Province. These two species come from *Aquilaria* trees in tropical regions. This data may indicate that this genus exhibits host-specificity. However, only two species have been discovered in this genus, which is insufficient to confirm this feature, and this needs more research.

This study provides a phylogenetic tree (Fig. 5) of Pleosporales to determine the position of *Mangifericomes*. After multiple constructions of multi-gene phylogenetic trees, we found that the placement of *Mangifericomes* is highly unstable and has low statistical support with other branches. Therefore, we still classify it as a Pleosporales genus *incertae sedis* (Wijayawardene et al. 2022), and more samples of the genus need to be collected to determine the taxonomic placement. *Mangifericomes aquilariae* is morphologically consistent with the monotypic genus introduced by Yang et al. (2022) and also forms a distinguishable sister branch with the type species *M. hongheensis* in the phylogenetic tree (Fig. 5). *Mangifericomes aquilariae* differs from *M. hongheensis* in morphology and significant differences in the comparison of basepair fragments (Jeewon and Hyde 2016). *Mangifericomes hongheensis* was found on *Mangifera indica* in Honghe, Yunnan Province, while *M. aquilariae* was found on *Aquilaria* sp. in Nujiang, Yunnan Province. Currently, both species have been isolated from broad-leaved tree species in tropical regions of China. Further research is needed to explore whether the distribution range of this genus is related to tropical plants.

Most members of Ascomycota are saprobes; the phylum is one of the most representative fungal communities involved in saprobic behavior (Benny et al. 2001; Li et al. 2022). The abundance of Ascomycota is higher in tropical forests than in other forest ecosystems (Tedersoo et al. 2014; Li et al. 2022; Hyde et al.

2024b). In order to more systematically fill the gap where only a few saprophytic fungi have been found in *Aquilaria*, in this study, we introduce two new terrestrial saprobic fungal species belonging to the Pleosporales in Ascomycota, which enrich the diversity of saprobic fungi on *Aquilaria*. For the first time, this study lists a comprehensive set of saprobic fungi associated with *Aquilaria* spp., laying a solid foundation for future research on taxa associated with *Aquilaria*.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: SCK, ST. Data curation: TYD. Formal analysis: SCK. Funding acquisition: DQD, ST, HHW. Investigation: SCK, ST, TYD. Methodology: SCK, ST, LSH, TYD. Project administration: ST, DQD, HHW. Resources: TYD. Software: TYD. Validation: SCK, SN, ST, KCR, KDH. Visualization: TYD. Writing—original draft: TYD. Writing—review and editing: SN, KDH, AM, LSH, AME, KCR, SCK, ST, TYD, DQD, HHW.

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Data availability

All of the data that support the findings of this study are available in the main text.

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